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THE VALIDITY OF *LAGOSUCHUS TALAMPAYENSIS* ROMER, 1971 (ARCHOSAURIA, DINOSAURIFORMES), FROM THE LATE TRIASSIC OF ARGENTINA

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ABSTRACT.   The Chañares Formation (latest Middle–earliest Late Triassic) of northwestern Argentina is part of the Ischigualasto–Villa Unión Basin and preserves a rich fossil vertebrate record discovered by a crew of the Museum of Comparative Zoology (Harvard University) led by Alfred Romer. A diverse non-dinosaurian dinosauromorph assemblage has been described from this formation and includes the iconic, small-sized "proto-dinosaur" *Lagosuchus talampayensis* Romer, 1971. This species has been crucial to understand the body plan of dinosaur precursors and the higher-level phylogenetic relationships of dinosaurs. More recently, authors considered this genus and species as *nomina dubia*. The aim of this contribution is to reassess the taxonomic validity of *L. talampayensis*. New observations indicate that the holotype of *L. talampayensis* differs from other avemetatarsalians, but not from the hypodigm of *Marasuchus lilloensis*, in the presence of a globose femoral head (strongly convex proximal and medial surfaces) with a distinctly dorsal orientation and a sub-oval outline in proximal view as a result of incipient posterior and posteromedial tuberosities. Thus, *Lagosuchus talampayensis* is here considered a senior synonym of "*Marasuchus lilloensis*" (Romer, 1972). Our conclusions have implications in the knowledge about early dinosauromorph diversity and the taxonomic richness of the group in the Chañares Formation.

KEY WORDS: Triassic; La Rioja province; Argentina; Avemetatarsalia; Dinosauriformes; *Marasuchus lilloensis*

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INTRODUCTION

The Ischigualasto–Villa Unión Basin is an extensive succession of late Permian–Late Triassic sedimentary rocks that crops out in northwestern Argentina (San Juan and La Rioja provinces) and have yielded abundant fossil vertebrates (Reig, 1963; Romer, 1966; Bonaparte, 1971, 1997). The information provided by these fossils has become crucial to understanding the evolution of Triassic

vertebrate assemblages in southern Pangaea. The Chañares Formation (latest Ladinian?–early Carnian; Marsicano et al., 2015; Ezcurra et al., 2017) is one of the most fossiliferous stratigraphic units of the Ischigualasto–Villa Unión Basin, and its fossil content was discovered and originally excavated by a crew of the Museum of Comparative Zoology (MCZ, Harvard University) led by Alfred S. Romer from October 1964 until February 1965 (Romer, 1966; Romer and Jensen, 1966). The fossils collected during this early field trip, most of them housed in the MCZ, represent one of the most informative Triassic vertebrate assemblages worldwide. Subsequently, José F. Bonaparte and collaborators increased the sample of fossil vertebrates of this unit during the late 1960s and 1970s. As a result of these explorations, an important diversity of nondinosaurian dinosauromorphs (informally called dinosaur precursors or "protodinosaurs") was described, including *Lagerpeton chanarensis*, *Lagosuchus talampayensis*, *Lago. lilloensis* (= *Marasuchus lilloensis*), *Pseudolagosuchus major*, and *Lewisuchus admixtus* (Romer, 1971, 1972a,b; Bonaparte, 1975; Arcucci, 1987; Sereno and Arcucci, 1994a,b; Bittencourt et al., 2014).These taxa have been and still are of key importance to understanding the origin and early evolution of Dinosauria (e.g., Romer, 1971, 1972; Bonaparte, 1975, 1995; Benton, 1990a,b; Novas, 1992, 1996; Sereno and Arcucci, 1994a,b; Ezcurra, 2006; Irmis et al., 2007; Nesbitt et al., 2010, 2017; Bittencourt et al., 2014; Cabreira et al., 2016).

Alfred Romer (1971) briefly described and erected the new, long-limbed dinosauromorph species *Lago. talampayensis* and *Lage. chanarensis* as part of a series of 20 contributions published in *Breviora* between 1966 and 1973 about the Chañares reptile fauna. *Lagosuchus talampayensis* is based on an associated, articulated partial vertebrl

column, pectoral girdle and forelimb and the pelvic bones associated with the right and left articulated hindlimbs of the same individual (Romer, 1971; Sereno and Arcucci, 1994). Romer (1971) proposed that this taxon was bipedal and that it may be related to the origin of "coelurosaurian" (cf. Coelophysoidea) theropods based on tarsal characters. Subsequently, Romer (1972) referred additional specimens to *Lago. talampayensis* and also erected the new species *Lago. lilloensis*. Regarding the holotype of this new species, Romer (1972: 5) stated that "except for larger size, the hind leg elements closely resemble those of the type. I felt justified in concluding that the two were specifically identical," but he concluded that "we have three specimens of femur of holotype size, only one larger. It is highly improbable that in a collection there would be three immature forms against only one adult. ... I am therefore forced to the conclusion that the present specimen represents a distinct species of *Lagosuchus*." Some years later, Bonaparte (1975) described in detail all available specimens of *Lago. talampayensis* housed in the MCZ and the Instituto Miguel Lillo (PVL) in Argentina and proposed that the size differences with *Lago. lilloensis* were not enough to support its taxonomic distinctiveness. Thus, Bonaparte (1975) considered *Lago. talampayensis* a senior synonym of *Lago. lilloensis*, and this conclusion was followed by subsequent authors in the 1980s and early 1990s (Arcucci, 1987; Novas, 1989, 1993; Benton, 1990a,b).

Sereno and Arcucci (1994) revised in detail both species and concluded that *Lago. talampayensis* was based on a nondiagnostic holotype and considered this genus and species nomina dubia. As a result, Sereno and Arcucci (1994) erected the new genus *Marasuchus* for the species "*Lago.*" *lilloensis*, resulting in the new combination *M. lilloensis* (Romer, 1972). Most subsequent authors

have followed this criterion (e.g., Novas, 1996, 2009; Ezcurra, 2006; Langer and Benton, 2006; Langer et al., 2013; Bittencourt et al., 2014), but one exception was a paper by Bonaparte (1995), in which he sustained the validity of *Lago. talampayensis* and considered *M. lilloensis* its junior synonym. As a consequence, the aim of this contribution is to revaluate the taxonomic validity of *Lago. talampayensis* and its synonymy with *M. lilloensis*. A full revision of the alpha taxonomy of the other dinosauromorphs of the Chañares Formation will be the subject of future contributions based on recently collected specimens (e.g., Novas et al., 2015; Ezcurra et al., 2018).

PALEONTOLOGICAL AND GEOLOGICAL SETTINGS

All available specimens of *Lago. talampayensis* and *M.* (= *Lagosuchus*) *lilloensis* come from the *Massetognathus-Chanaresuchus* Assemblage Zone (AZ) of the lower member of the Chañares Formation (Romer, 1971, 1972; Bonaparte, 1975; Sereno and Arcucci, 1994; Ezcurra et al., 2017). Romer and Jensen (1966) recognized the outcrops of the Chañares Formation in the area delimited between the Talmapya, Chañares, and Gualo rivers, and this unit was traditionally dated as Ladinian (Bonaparte, 1997; Rogers et al., 2001). More recently, Desojo et al. (2011) proposed that the deposition of the Chañares Formation may have extended into the Carnian, a statement that was recently bolstered by radioisotopic dating that constrained the dated levels of the unit as lower Carnian (Marsicano et al., 2015; Ezcurra et al., 2017). However, the still undated first 10–15 m of the unit (*Tarjadia* AZ) may extend back into the latest Ladinian (Ezcurra et al., 2017).

The outcrops of the Chañares Formation that yielded specimens of *Lagosuchus* and *Marasuchus* belong to a locality (northwest pocket of Romer field notes 1964–1965 or classic Los Chañares locality of Rogers et al. [2001]) placed 3 km north of the Chañares River and 5 km southwest of the Puerta de Talampaya (Romer, 1971, 1972; Bonaparte, 1975; Sereno and Arcucci, 1994). These dinosaur precursor fossils come from subspherical concretions between 30 and 250 cm in diameter (Mancuso et al., 2013), placed approximately 10–15 m above the base of the sedimentary column at the Chañares type locality (Ezcurra et al., 2017: supplementary fig. 4). These concretions contain abundant vertebrate fossils that have been well known since the 1960s and include abundant and usually articulated, fairly complete skeletons of proterochampsids, gracilisuchid and dinosauromorph archosaurs, dicynodonts, and chiniquodontid and early probainognathian cynodonts (Romer and Jensen, 1966; Bonaparte, 1997; Rogers et al., 2001; Krapovickas et al., 2013; Mancuso et al., 2013; Marsicano et al., 2015; Ezcurra et al., 2017). The dinosauromorph assemblage of the Chaares Formation includes the lagerpetid *Lage. chanarensis* and the nondinosaurian dinosauriforms *Lago. talampayensis*, *Lago. lilloensis* (= *Marasuchus lilloensis*), *Ps. major*, and *Le. admixtus* (Romer, 1971, 1972b; Arcucci, 1987). Several authors have considered that *Le. admixtus* may represent a subjective senior synonym of *Ps. major* (Arcucci, 1997; Nesbitt et al., 2010; Bittencourt et al., 2014; Novas et al., 2015; Ezcurra, 2016; Ezcurra et al., 2018).

Institutional abbreviations

GR, Ghost Ranch Ruth May Museum of Paleontology, New Mexico, USA; ISIR, Indian Statistical Institute, Kolkata, India; MACN-Pv, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Paleontología de Vertebrados, Buenos Aires, Ar-

Figure 1. *Lagosuchus talampayensis* Romer, 1971 (PULR 09, holotype). Incomplete skeleton (top) and interpretative drawing (bottom) modified from Sereno and Arcucci (1994). Bones of *Lago. talampayensis* indicated in black. Abbreviations: lf, left foot; lfe, left femur; lfi, left fibula; lhu, left humerus; lis, left ischium; lpu, left pubis; lra, left radius; lsc, left scapula and coracoid; lti, left tibia; rfe, right femur; rfi, right fibula; rpu, right pubis; rti, right tibia. *Scale bar:* 2 cm.

gentina; MLP, Museo de La Plata, La Plata, Argentina; MCZ, Museum of Comparative Zoology, Cambridge, USA; NHMUK PV, The Natural History Museum, Palaeontology Vertebrates, London, UK; NMT, National Museum of Tanzania, Dar es Salaam, Tanzania; PULR, Paleontología, Universidad Nacional de La Rioja, La Rioja, Argentina; PVL, Paleontología de Vertebrados, Instituto "Miguel Lillo," San Miguel de Tucumán, Argentina. PVSJ, División de Paleontología de Vertebrados del Museo de Ciencias Naturales y Universidad Nacional de San Juan, San Juan, Argentina; QG,

Queen Victoria Museum, Department of Paleontology, Harare; SAM-PK-K, Iziko South African Museum, Cape Town, South Africa; SMNS, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; UFRGS-PV, Universidade Federal do Rio Grande do Sul, Porto Alegre, RS, Brazil; ULBRA-PVT, Universidade Luterana do Brazil, Canoas, Brazil; USNM, National Museum of Natural History (formerly United States National Museum), Smithsonian Institution, Washington, D.C., USA; ZPAL, Institute of Paleobiology of the Polish Academy of Sciences, Warsaw, Poland.

SYSTEMATIC PALEONTOLOGY

Archosauria Cope, 1869, *sensu* Gauthier and Padian, 1985

Avemetatarsalia Benton, 1999

Dinosauriformes Novas, 1992, *sensu* Nesbitt, 2011

Lagosuchus Romer, 1971

Lagosuchus talampayensis Romer, 1971

= "*Lagosuchus lilloensis*" new species Romer, 1972

= "*Marasuchus lilloensis*" new genus and new combination Sereno and Arcucci, 1994

Holotype. PULR 09, partial postcranium composed of the last eight dorsal and two sacral vertebrae in articulation (see Description); first seven caudal vertebrae articulated or in close proximity; a partial middle-distal caudal vertebra; articulated left scapula, coracoid, humerus, radius, and ulna; partial pelvic girdles; articulated right femur, tibia, and fibula (the latter two lacking their distal ends); and most of the articulated left hindlimb lacking the proximal half of the femur and most phalanges (Fig. 1). The left hindlimb is labeled with the same number (PULR 08) as the holotype of the pseudosuchian *Gracilisuchus stipanicicorum* Romer (1972).

Referred Specimens. MCZ 4137 (originally catalogued as MCZ 4116), a series of 17 presacral vertebrae, partial sacrum, right ilium and pubis, and right femur articulated with proximal end of tibia; PVL 3870, partial skeleton including left maxilla, partial braincase, vertebral column from the atlas to anterior caudal vertebrae, articulated pelvis and hindlimbs lacking distal phalanges; PVL 3871, partial articulated skeleton including the last dorsal vertebra to the 25th caudal vertebra, left scapulocoracoid, humerus, radius, and ulna, right hemipelvis, left ilium and pubis, partial right and left hindlimbs (holotype of "*M. lilloensis*"); PVL 3872, articulated partial right squamosal and quadrate (the ventral two-thirds of the quadrate are currently lost), partial braincase, and vertebral column from the atlas to the ninth presacral vertebra; PVL 4671, articulated anterior caudal vertebrae with haemal arches; PVL 4672, articulated vertebral column from atlas to the 17th presacral vertebra, right scapula and coracoid, and left humerus.

Revised Diagnosis. Lagosuchus talampayensis is a small dinosauromorph (largest known femoral length of 57.5 mm; PVL 3871) that differs from closely related species, such as *Le. admixtus, Asilisaurus kongwe,* and *Silesaurus opolensis,* in the presence of the following autapomorphies: femoral head with strongly convex proximal and medial surfaces, acquiring a globose overall shape (the femoral head of other avemetatarsalians possesses straight proximal and medial surfaces in anterior and posterior views; modified from Bonaparte, 1975) (present in PULR 09, MCZ 4137, PVL 3870, and PVL 3871); iliac ischiadic peduncle with straight ventral margin (other early avemetatarsalians, such as *Si. opolensis, A. kongwe,* and *Teleocrater rhadinus,* possess a ventrally notched ischiadic peduncle, suggesting the persistence of small acetabulum

perforations; Nesbitt et al., 2017) (unknown in PULR 09, present in PVL 3870 and PVL 3871); and transversely concave posterior surface of distal end of pubic apron (flat in other early avemetatarsalians; Sereno and Arcucci, 1994) (unknown in PULR 09, present in PVL 3870 and PVL 3871).

Furthermore, *Lago. talampayensis* may be distinguished from other early dinosauriforms by having the combination of fan-shaped dorsal neural spines in lateral view that contact adjacent spines and lack flattened ossifications roofing them (fan-shaped neural spines contacting adjacent spines are also present only in *Le. admixtus* among nondinosaurian dinosauriforms, but this species possesses a row of imbricated ossifications roofing these spines; Sereno and Arcucci, 1994; Bittencourt et al., 2014) (present in PULR 09, MCZ 4137, PVL 3870, PVL 3872, and PVL 4672).

Beyond the presence of these characters, the hypodigm of *Lago. talampayensis* can be distinguished from other avemetatarsalians by the combination of the following character states: haemal arches three times longer dorsoventrally than the anteroposterior length of their respective caudal centra in the proximal portion of the tail (unknown in *Le. admixtus;* Sereno and Arcucci, 1994) (unknown in PULR 09, present in PVL 3870 and PVL 4671), coracoid foramen opening laterally and medially ventral to the scapulacoracoid suture (foramen absent in *Le. admixtus*) (unknown in PULR 09, present in PVL 3871 and PVL 3872), absence of brevis fossa on the ilium (fossa present in silesaurids) (unknown in PULR 09, present in specimens MCZ 4137, PVL 3870, and PVL 3871), and straight fourth metatarsal in anterior and posterior views (laterally curved in dinosaurs and *Si. opolensis;* Novas, 1996; Dzik, 2003) (present in PVL 3870 and PVL 3871).

Lagosuchus talampayensis is clearly distinguished from lagerpetids, such as *Lage. chanarensis*, by lacking a deep emargination at the base of the femoral head; femoral head globose that lacks a strong anteroposterior compression, being not hook-shaped; lacking an hypertrophied tibiofibular crest in the distal end of the femur; and lacking a posterior ascending process in the astragalus (see Sereno and Arcucci, 1994a; Nesbitt, 2011). Additionally, when compared with the holotype specimen of *Ps. major* (PVL 4629), the holotype of *Lago. talampayensis* differs in the presence of a globose femoral head (i.e., strongly convex proximal and medial surfaces) (Arcucci, 1987).

Following our revised diagnosis of *Lago. talampayensis*, we are not able to refer a complete left scapulacoracoid (MCZ 9483)—previously referred to *Lago. talampayensis* by Romer (1972)—and a series of articulated anterior caudal vertebrae lacking haemal arches (PVL 4670)—previously referred to "*M. lilloensis*" by Sereno and Arcucci (1994)—because of the absence of autapomorphies or a unique combination of character states that may support their species-level assignment.

DESCRIPTION

The holotype of *Lago. talampayensis* (PULR 09, including the left hindlimb labeled as PULR 08; the entire specimen is hereafter referred as PULR 09 for simplicity) was described by Romer (1971, 1972) and Sereno and Arcucci (1994). Here we expand these descriptions with new detailed anatomical information to allow revisiting the validity of *Lago. talampayensis*. The holotype of "*M. lilloensis*" and its referred specimens have been described and figured in detail by Bonaparte (1975) and Sereno and Arcucci (1994); therefore, we consider a

redescription is not required for the purpose of this manuscript.

PULR 09 is preserved mixed with the larger, partially articulated skeletons of the holotype of the pseudosuchian *G. stipanicicorum* (PULR 08) and a referred specimen of the proterochampsid *Tropidosuchus romeri* (PULR unnumbered) (Romer, 1971; Sereno and Arcucci, 1994). The holotype of *Lago. talampayensis* is represented by a partial left pectoral girdle and forelimb, a complete series of 17 vertebrae, and partially flexed hindlimbs, which are preserved resembling the resting pose described for other dinosauriforms (Fig. 1; Agnolin and Martinelli, 2015). The presacral and sacral vertebrae are preserved in articulation, and the anterior caudal vertebrae, pelvic girdle, and hindlimbs are in approximate anatomical position—although not articulated. The partial pectoral girdle and forelimb lie 3 cm in front of the preserved dorsal series, but the size and position of these bones in the slab strongly suggest that they belong to the same individual, as originally interpreted by Romer (1971). There is no evidence of gastral elements or osteoderms.

Dorsal Vertebrae. The preserved eight distalmost dorsal vertebrae probably correspond to the 7th–8th to 14th–15th vertebrae of the trunk series if we consider, as occurs in other Triassic dinosauriforms, a presacral column composed of 23 or 24 vertebrae, in which nine are cervical vertebrae and 14–15 are dorsal vertebrae (Bonaparte, 1975; Piechowski and Dzik, 2010). Damage and some areas covered with matrix obscure several features of the dorsal vertebrae. The preserved vertebral centra are strongly elongated, being approximately three times longer anteroposteriorly than the dorsoventral height of the anterior and posterior facets (Fig. 2). This ratio resembles, but slightly exceeds, that of the middle-distal dorsal vertebrae of a specimen referred to "*M.*
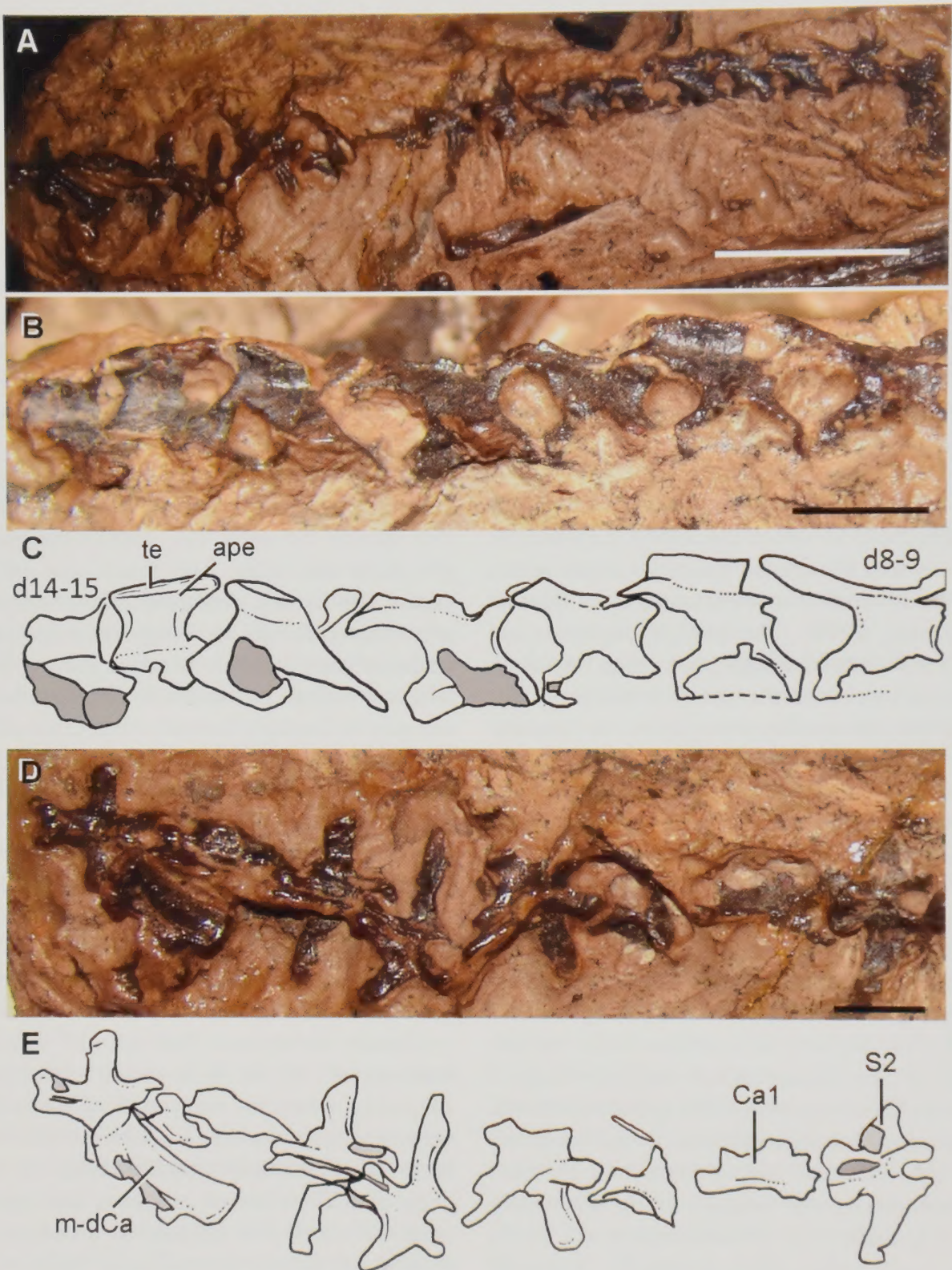
Figure 2.   Vertebral column of *Lagosuchus talampayensis* (PULR 09, holotype) in A. anterodorsal and dorsal views; B, C. detail of dorsal vertebrae in right lateral view; D, E. detail of sacral 2 and caudal vertebrae in dorsal view. Light grey areas indicate broken surface. Abbreviations: ape, anteroposterior expansion; Ca 1, first caudal vertebra; d8-9, dorsal vertebra 8 or 9; d14-15, dorsal vertebra 14 or 15; m-dCa, middle-distal caudal vertebra; S2, second sacral vertebra; te, transverse expansion. *Scale bars:* A. *2 cm;* B, D. 5 mm.

lilloensis" by Sereno and Arcucci (1994; ratio approximately 2.3 in the most elongated dorsal vertebrae of PVL 3870; in other specimens this ratio is even lower). The vertebral centra and the bases of the neural arches are laterally excavated immediately ventral to the diapophyses, a condition listed in the original diagnosis of "*M. lilloensis*" (Sereno and Arcucci, 1994) and widespread among several archosauromorph lineages (Ezcurra, 2016), including other dinosauriforms (Bonaparte, 1995, 1997). The diapophyses are horizontal and subtriangular in dorsal view, being anteriorly displaced from the mid-length of the neural arch. The parapophyses are placed close to the diapophyses and are connected to the latter by a short and thin paradiapophyseal lamina, as occurs in several archosauromorphs (Ezcurra et al., 2014). The prezygapophyses are oriented anterodorsally and extend approximately level with the anterior margin of the centrum. The postzygapophyses are horizontal in lateral view and extend distinctly beyond the margin of the centrum. The preserved bases of the neural spines are long anteroposteriorly and extend along most of the anteroposterior length of the neural arch. Only the 13th or 14th dorsal vertebra preserves a complete neural spine, and the dorsal half is expanded anteroposteriorly, with a more developed and tapering anterior end. The degree of anteroposterior expansion of the neural spine indicates that it should have contacted its adjacent spines. This condition was included in the diagnosis of "*M. lilloensis*" by Sereno and Arcucci (1994) and is also present in the dinosauriform *Le. admixtus* (Bittencourt et al., 2014). The top of this spine is gently thickened transversely, as occurs in a referred specimen of "*M. lilloensis*" (PVL 3870), *Le. admixtus* (Bittencourt et al., 2014), and *Si. opolensis* (Piechowski and Dzik, 2010). PULR 09 lacks ossifications roofing the dorsal end of the

neural spines, as occurs in other nondinosaurian avemetatarsalians, but contrasting with the condition in *Le. admixtus* (Bittencourt et al., 2014).

Sacral Vertebrae and Ribs. The two sacral vertebrae and their partial ribs are exposed in dorsal view (Fig. 2). The subsequent vertebra of the series is very poorly preserved, and it is not possible to determine whether it belongs to the sacral region or represents the first caudal. However, we assume the presence of two sacral vertebrae in PULR 09 because this condition is present in specimens previously referred to "*M. lilloensis*" (Bonaparte, 1975; Sereno and Arcucci, 1994). It is not possible to discern the suture between the sacral transverse processes and ribs. The distal end of the sacral ribs is not preserved. The transverse processes and ribs are long and trapezoidal in dorsal view, slightly broader at their base. The transverse processes of the first sacral are oriented mainly laterally, but those of the second sacral possesses a distinct posterolateral orientation. The preserved base of the neural spines is short anteroposteriorly and displaced posteriorly on the neural arch. The prezygapophyses are well separated from each other by a wide, U-shaped notch. The postzygapophyses are very close to the median line and extend only slightly beyond the base of the neural spine.

Caudal Vertebrae. The caudal series is represented by its first seven vertebrae—assuming a sacrum composed of two sacral vertebrae (see above)—and an isolated centrum of a probable middle-distal element (Fig. 2). The proximal vertebrae are exposed in dorsal view. The transverse processes are subrectangular and very long in dorsal view, representing 0.85 times the anteroposterior length across zygapophyses in the fourth caudal. These processes become shorter posteriorly in the series, and those of the seventh caudal are less than half their length

in the fourth caudal. The prezygapophyses are long and oriented anterodorsally, as occurs in the anterior caudal vertebrae of the holotype of "*M. lilloensis*" (PVL 3871). The prezygapophyses of PULR 09 are separated from each other by a broad U-shaped interprezygapophyseal notch. The prezygapophyses are connected to the neural spine through weak spinoprezygapophyseal laminae. The postzygapophyses are very short and separated from each other by a shallow median cleft in dorsal view. The neural spines are relatively low and extend along the entire median line of the neural arch. The neural spine extends posteriorly, level with the posterior margin of the short postzygapophyses.

The centrum of the middle-distal caudal vertebra is approximately three times longer than tall and around 1.2 times longer than the neural arch of the anterior caudal vertebrae. Middle-distal caudal vertebrae distinctly longer than the proximal caudal vertebrae also occur in the holotype and previously referred specimens of "*M. lilloensis*" (PVL 3870, PVL 4671; Sereno and Arcucci, 1994). The middle-distal centrum of PULR 09 is slightly constricted transversely around mid-length and the articular surfaces are subcircular and concave. The presence of a ridge or groove on the ventral surface of the centrum cannot be determined. A longitudinal depression occurs along the transition between the centrum and neural arch.

Pectoral Girdle. The partial left scapula and coracoid are preserved in medial view and natural position to each other, but it is not possible to discern whether they were fused (Fig. 3). Damage obscures several anatomical features. The preserved portion of the scapular blade expands gradually anteroposteriorly toward the distal end. The medial surface of the bone is slightly concave, with the exception of a low and broad longitudinal ridge that is slightly displaced from mid-width posteriorly at the base of the blade. A similar ridge is present in some other early dinosauriforms (e.g. *Le. admixtus*: PULR 01; *Herrerasaurus ischigualastensis*: PVSJ 373; *Megapnosaurus rhodesiensis*: QG 1). There are no informative traits to describe from the partial coracoid.

Forelimbs. The left humerus is exposed in anteromedial view, and the medial side of its proximal third and the distal end are damaged, precluding the description of the latter region (Fig. 3). It is a gracile bone, with a very slender shaft. Its proximal end is slightly expanded transversely and possesses a transversely concave anterior surface. This concavity is broad and subtriangular, with a distal apex, but relatively shallow, and should have housed the attachment for the musculus coracobrachialis brevis pars ventralis (Langer et al., 2007). This concavity is delimited laterally by a moderately long and low deltopectoral crest, whose base extends along approximately 31% of the length of the bone, resembling the condition in proterochampsids (e.g., *Chanaresuchus bonapartei*, PVL 4575: 31%; *T. romeri*, PVL 4604: 31%), the lagerpetid *Ixalerpeton polesinensis* (ULBRA-PVT059: 35%), and several pseudosuchians (e.g., *Parasuchus hislopi*, ISIR collection: 35%; *Nicrosaurus kapffi*, SMNS collection: 32%; *Smilosuchus gregorii*, USNM 18313: 28%; *Aetosauroides scagliai*, PVL 2073: 33%; *A. scagliai*, PVL 2091: 30%; *Prestosuchus chiniquensis*, UFRGS-PV-0152T: 34%). By contrast, the deltopectoral crest is proportionally longer in other avemetatarsalians, including aphanosaurians (e.g., *Yarasuchus deccanensis*, ISIR 334/53: 49%; *T. rhadinus*, NMT RB476: 44%), pterosaurs (e.g., *Dimorphodon macronyx*; Padian, 1983: fig. 8: 46%), the holotype of "*M. lilloensis*" (PVL 3871: ca. 40%), *Le. admixtus* (PULR 01: >37%), *Si. opolensis* (ZPAL Ab/III/452: 38%), and dinosaurs

Figure 3.   Left pectoral girdle and forelimb of *Lagosuchus talampayensis* (PULR 09; holotype). Photograph (top) and interpretative drawing (bottom). Light grey areas indicate broken surface, and dark grey elements are bones that do not belong to *Lago. talampayensis*. Abbreviations: dpc, deltopectoral crest; hh, humeral head; ra, radius; ri, medial ridge; sc, scapula; ul, ulna. *Scale bar:* 5 mm.

(e.g., *Her. ischigualastensis*, MACN-Pv 18060: 52%; *Heterodontosaurus tucki*, SAM-PK-K1332: 42%). The deltopectoral crest is subtriangular in lateral and medial views, and its apex is placed approximately 20% down the length of the bone, as occurs in other nondinosaurian archosauriforms, in which the apex is placed not beyond 30%

down the bone (Langer and Benton, 2006; Nesbitt, 2011). The deltopectoral crest seems to be slightly displaced distally from the proximal margin of the bone and is connected with the head by a relatively narrow edge.

The radius and ulna are exposed in medial view. Their distal ends are partially covered with matrix and bones of the specimen of *T.*

romeri (Sereno and Arcucci, 1994). The medial surface of the proximal end of the radius possesses a broad concavity that received the ulna. The proximal end of the ulna is subtriangular in medial view and lacks an olecranon process, contrasting with the well-developed olecranon of the holotype of "*M. lilloensis*" (Bonaparte, 1975; PVL 3871). The shaft of both bones is nearly straight, and their distal ends are slightly expanded anteroposteriorly. The length of the radius and ulna is 65% that of the humerus, and as a result, the anterior zeugopodium of PULR 09 is proportionally shorter than that of the holotype of "*M. lilloensis*" (PVL 3871: >72%) and most archosauriforms (Ezcurra, 2016). Indeed, such a low ratio between radius and humerus is an uncommon condition among archosauriforms and occurs in only a few taxa (e.g., *Vancleavea campi*, Nesbitt et al., 2009, fig. 13: 62%; *Par. hislopi*, Chatterjee, 1978, table 2: 67%).

Pelvic Girdle. The pelvic girdle of PULR 09 is incomplete and extensively covered with matrix, thus it provides considerably less information than the other dinosauriform specimens from the Chañares Formation described in detail by Bonaparte (1975) and Sereno and Arcucci (1994). The pelvic region of PULR 09 is represented by probable iliac fragments preserved close to the femoral head, partial left and right pubes (exposed in lateral and anterior views, respectively), and a fragmentary left ischium exposed in lateral view (Fig. 4).

The morphology of the pubis and ischium is congruent with that of the referred specimen of "*M. lilloensis*" PVL 3870. The pubis of PULR 09 possesses a distinct iliac peduncle that finishes into a concave articular surface for the ilium. The pubic shaft possesses a moderately transversely broad and dorsoventrally thin apron. The proximal end of the ischium is long anteroposteriorly,

indicating an extensive contribution to the acetabulum. The acetabular margin of the ischium is nearly straight. It is not possible to determine the presence of the antitrochanter present in PVL 3870 because of damage. The rest of the ischium is plate-like, with the exception of a thick, rounded ridge adjacent to the posterior margin of the shaft. The ventral lamina below this ridge is well developed, as also occurs in PVL 3870 and other dinosauriforms (Novas, 1996; Nesbitt, 2011). The posterior margin of the shaft is distinctly concave. The distal end of the ischium is missing and/or covered with epoxy.

Hindlimbs. The right hindlimb includes a complete femur articulated with the tibia and fibula (Figs. 1, 4, 5). The latter two bones lack their distal ends. The left hindlimb is also articulated and more complete, lacking the proximal half of the femur and several phalanges. The proximalmost phalanges of digits I–III are articulated to their respective metatarsals, and there are three other phalanges disarticulated, but in close association with the right foot. It is not possible to determine the identity of these phalanges and, as a consequence, either the total length or phalanx count of any digit.

The morphology of the femur of PULR 09 is almost identical to that of "*M. lilloensis*" (PVL 3870, 3871; Bonaparte, 1975; Sereno and Arcucci, 1994). The femur is distinctly sigmoid in lateral view, with posteriorly and anteriorly bowed proximal and distal halves, respectively (Fig. 5). By contrast, the bone is mostly straight in anterior view, with the exception of a sharply posterolaterally flexed proximal end. The femoral shaft is very narrow and reaches its minimum width at the level of the distal end of the fourth trochanter in anterior view. The femoral head is oriented anteromedially (if it is considered that the distal condyles are posteriorly projected) and forms a broad

Figure 4. Partial pelvic girdle and right hindlimb of *Lagosuchus talampayensis* (PULR 09, holotype). Photograph (left) and interpretative drawing (right). Light grey areas indicate broken surface, and dark grey elements are bones that do not belong to *Lago. talampayensis*. Abbreviations: as, acetabular surface; Cas, caudal vertebrae; Ds, dorsal vertebrae; lis, left ischium; lp, left pubis; rfe, right femur; rfi, right fibula; ri, ridge; ril, right ilium; rpu, right pubis; rti, right tibia; sa, sacral vertebrae. *Scale bar:* 1 cm.

and moderately deep concavity with the shaft in posteromedial and anterolateral views, thus being distinctly projected from the neck, resembling the condition in *Le. admixtus* (PULR 053) and "*M. lilloensis*" (PVL 3870, 3871). However, the femoral head of *Lago. talampayensis* projects less than in lagerpetids (e.g., *Lage. chanarensis*: MCZ 4121, PULR 06, PVL 4619; *Dromomeron romeri*: GR 218; *I. polesinensis*: ULBRA-PVT059). The femoral head of PULR 09 is subtly oriented more proximomedially than in the holotype and a referred specimen of "*M. lilloensis*" (PVL 3870, 3871) and *Le. admixtus* (PULR 053). The femoral head is distinctly globose as a result of strongly convex proximal and medial artic-

ular surfaces, as also occurs in "*M. lilloensis*" (PVL 3870, 3871) and lagerpetids (e.g., *Lage. chanarensis*: MCZ 4121, PULR 06, PVL 4619; *D. romeri*: GR 218; *I. polesinensis*: ULBRA-PVT059). By contrast, the proximal articular surface of the femoral head is flat or incipiently convex in other early avemetatarsalians (e.g., *T. rhadinus*: NHMUK PV R6795; *Le. admixtus*: PULR 053; *Si. opolensis*: ZPAL Ab III/361/25; *A. kongwe*: Nesbitt et al., 2010). The articular surface extends distally on the posterior surface of the proximal end of the bone and is well-rimmed from the rest of the bone, indicating the probable presence of a cartilage cap, as also occurs in the holotype and a referred specimen of "*M. lilloensis*" (PVL
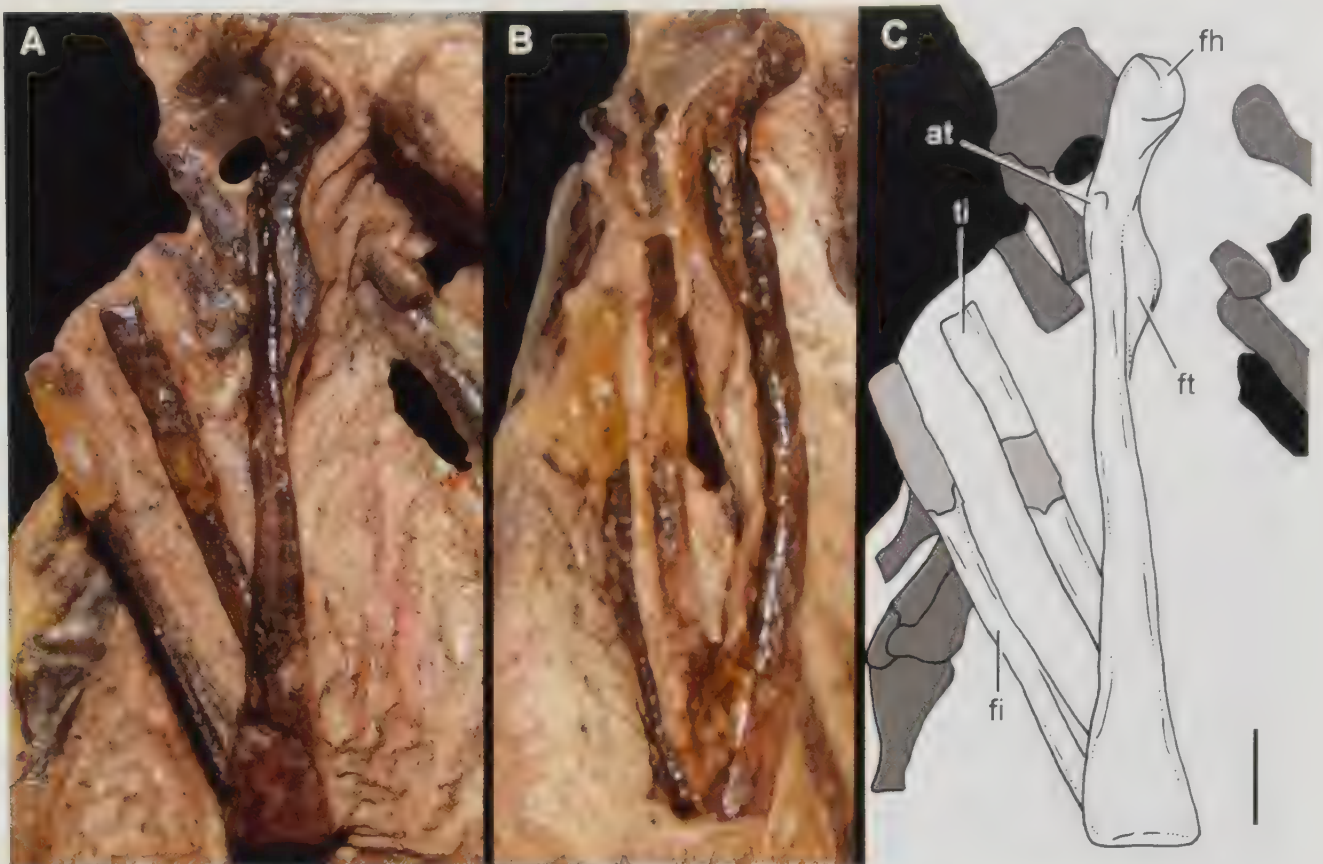
Figure 5.   Incomplete right hindlimb of *Lagosuchus talampayensis* (PULR 09, holotype) in A, C, anterior, and B. lateral views. Light grey areas indicate broken surface, and dark grey elements are bones that do not belong to *Lago. talampayensis*. Abbreviations: at, anterior trochanter; fh, femoral head; fi, fibula; ft, fourth trochanter; ti, tibia. *Scale bar:* 5 mm.

3870, 3871; Bonaparte, 1975; Sereno and Arcucci, 1994).

In the femoral shaft, the anterior trochanter is represented by a low, rounded projection placed in the anterolateral surface of the bone (Fig. 5). Damage in this area precludes the recognition—if present—of a trochanteric shelf and associated muscle scars. The fourth trochanter is placed immediately distal to the level of the base of the anterior trochanter and extends distally up to around the mid-length of the bone. This process is trapezoidal (i.e., symmetric) in anterior view, and the proximal and distal margins gently merge with the femoral shaft. The distal end of the bone is slightly expanded transversely and lacks an extensor fossa on the anterior surface. The distal condyles project posteriorly.

The tibia and fibula are poorly preserved and covered with matrix and other bones: thus, few informative anatomical details can be observed (Fig. 5). Both elements are gracile and possess a nearly straight shaft. The tibia is 1.1 times longer than the femur. The cnemial crest is low and projects anteriorly. The distal end of the tibia is anteroposteriorly deeper than transversely wide. A longitudinal groove runs along the lateral surface of the distal third of the bone and opens distally, as occurs in proterochampsids and dinosauriforms (Nesbitt, 2011). The fibular shaft is narrower than that of the tibia.

PULR 09 preserves a partial astragalar body and distal tarsals 3 and 4 (Fig. 6). The preserved portion of the astragalus is separated a few millimeters from the tibia but lies in articulation with distal tarsal 3 and the metatarsus. The anterior and ventral surfaces of the lateral portion of the astragalar body are strongly convex, and the rest of the exposed surface of the bone seems to be damaged. The morphology of the distal tarsals of PULR 09 is congruent with those of "*M. lilloensis*" (PVL 3870, 3871) and *Lage. chanarensis* (Sereno and Arcucci, 1994; Nesbitt, 2011). Distal tarsal 3 is a subspherical bone placed on the posterior half of the proximal surface of metatarsals II and III. Distal tarsal 4 is broader transversely and taller than distal tarsal 3 and articulates with the latter bone and metatarsals IV and V. The posterior portion of the proximal surface possesses a proximally raised "heel," as occurs in "*M. lilloensis*" (PVL 3870, 3871) and *Lage. chanarensis* (Sereno and Arcucci, 1994) but contrasts with the flat proximal surface of the bone present in nonarchosaurian archosauriforms, pterosaurs, and dinosaurs (Nesbitt, 2011). Distal tarsal 4 should have also articulated with the calcaneum, but the latter bone is not preserved in PULR 09.

The metatarsals are straight and closely appressed to each other. Metatarsal III is the longest and metatarsals I and V are distinctly shorter than the others. This condition resembles that of other dinosauriforms (e.g., *Si. opolensis*: Dzik, 2003) but differs from the metatarsus of *Lage. chanarensis*, in which metatarsal IV is the longest (Fig. 6; Sereno and Arcucci, 1994a). Metatarsal I is longer than metatarsal V, but the inverse occurs in the referred specimen of "*M. lilloensis*" PVL 3870. Metatarsals I–IV of PULR 09 are subequal in thickness, but the proximal end of metatarsal V is considerably broader and plate-like, resembling the condition in *Lage. chanarensis* (Sereno and

Arcucci, 1994a) and PVL 3870. The proximal end of the medial metatarsals partially overlaps the lateral ones in posterior view. Metatarsal V extends proximally beyond the level of the other metatarsals, as occurs in other early avemetatarsalians (e.g., *Powellvenator podocitus*: Ezcurra, 2017). Metatarsals I–IV possess deep collateral ligamental pits. Metatarsal I has a transversely compressed proximal half that results in an oval cross section, with an anteroposteriorly oriented main axis. The shaft of metatarsal V possesses a transversely concave posterior surface and strongly tapers distally, ending in an acute tip without a distal articular surface, as occurs in *Lage. chanarensis* (Sereno and Arcucci, 1994a) and PVL 3870 (Fig. 6).

The preserved phalanges are long and slender. Phalanges I-1 and II-1 are subequal in length, and phalanx III-1 is distinctly longer (Sereno and Arcucci, 1994). These phalanges are transversely compressed around mid-length and their distal ends possess a well-developed trochlea. The best exposed pedal ungual—the phalanx preserved furthest from the metatarsus—is gently curved and slightly shorter than phalanx II-1 (Table 1). This ungual is weakly transversely and dorsoventrally compressed. The lateral surface possesses a single lateral groove, and the ventral surface lacks a flexor tubercle.

DISCUSSION

Validity of *Lago. talampayensis* and taxonomic status of "*M. lilloensis*"

Sereno and Arcucci (1994) diagnosed "*M. lilloensis*" on the basis of a unique combination of character states. These authors considered that none of these diagnostic traits could be confidently determined in the holotype of *Lago. talampayensis* (PULR
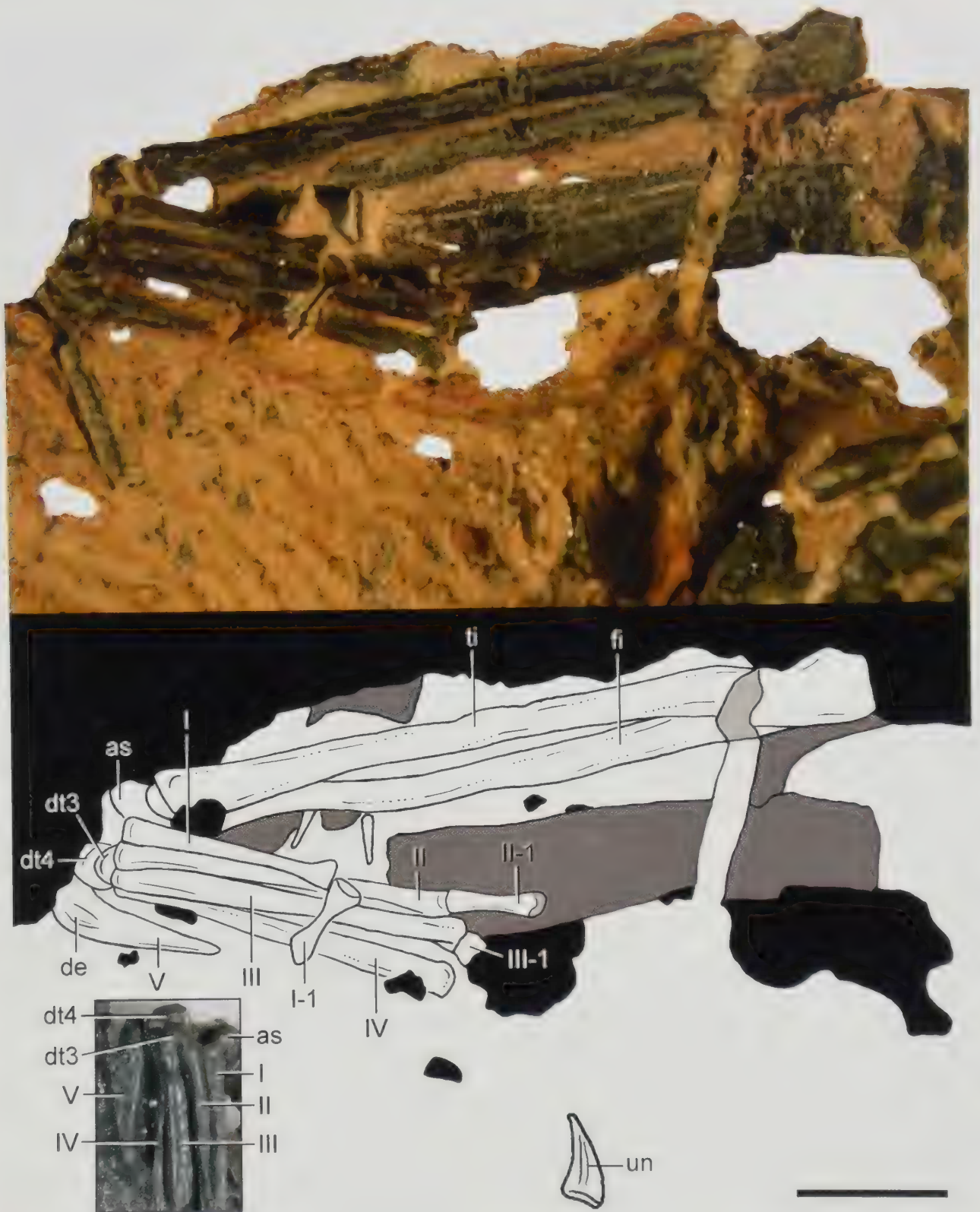
Figure 6.   Incomplete left hindlimb of *Lagosuchus talampayensis* (PULR 09, holotype) in anteromedial view (tibia, fibula, and astragalus) and ventral view (distal tarsals and foot). Close-up of the tarsus and proximal half of the metatarsus in ventral view in the left bottom corner of the figure. Abbreviations: I–V, first to fifth metatarsals; I-1, first phalanx of first digit; II-1, first phalanx of second digit; III-1, first phalanx of third digit; as, astragalus; de, depression; dt3, distal tarsal 3; dt4, distal tarsal 4; fi, fibula; ti, tibia; un, ungual phalanx. *Scale bar:* 1 cm.

TABLE 1. SELECTED MEASUREMENTS OF THE HOLOTYPE OF
LAGOSUCHUS TALAMPAYENSIS (PULR 08, 09).

Bone	Length (mm)	Width (mm)
Humerus	28	—
Radius	18	—
Femur	41	—
Tibia	46.6	—
Distal tarsal 3	—	2.2
Distal tarsal 4	—	3.1
Metatarsal I	14.3	—
Metatarsal II	22.5	—
Metatarsal III	24.1	—
Metatarsal IV	23.6	—
Metatarsal V	11.4	—
Phalanx I-1	6.6	—
Phalanx II-1	5.3	—
Ungual	5.1	—

09). However, the revision of this specimen leads us to consider that some features cited in the diagnosis of "*M. lilloensis*" are indeed present in PULR 09, such as a distinct fossa ventral to the transverse processes of the dorsal vertebrae and subtriangular neural spines in posterior dorsal vertebrae that contact each other anteriorly and posteriorly, although this feature is also present in *Le. admixtus* (PULR 01; Bittencourt et al., 2014). Nevertheless, there is a unique combination of character states shared between the holotypes of *Lago. talampayensis* and "*M. lilloensis*" that support their synonymy, namely dorsal vertebrae with fan-shaped neural spines that contact adjacent spines and lack flattened ossifications roofing them in lateral view, and femur with a globose (strongly convex proximal and medial surfaces) head with its long axis forming an angle of more than 60° with respect to the transverse axis through the femoral distal condyles (see Revised Diagnosis; Figs. 2, 7).

The presence of an anteroposteriorly expanded distal end of the presacral neural spines is a condition shared only by PULR 09, specimens previously included in the hypodigm of "*M. lilloensis*" (Sereno and Arcucci, 1994), and *Le. admixtus* (Bittencourt et al., 2014) among Triassic avemetatarsalians. However, *Le. admixtus* differs from PULR 09, "*M. lilloensis*," and other nondinosaurian avemetatarsalians in the presence of a median row of imbricate ossifications roofing these neural spines (Bittencourt et al., 2014). The absence of such ossifications in PULR 09 could be a result of lack of preservation. However, these ossifications are intimately appressed to the dorsal neural spines in *Le. admixtus* (PULR 01); as a result, if present, it would be expected that they were preserved above the complete neural spine of the 13th or 14th dorsal vertebra of PULR 09.

The globose femoral head of PULR 09 closely resembles that of the holotype and previously referred specimens of "*M. lilloensis*" PVL 3870 and PVL 3871. These femoral heads differ from those with a flatter proximal surface present in most other early avemetatarsalians (with the exception of lagerpetids) and the more medially developed femoral heads of lagerpetids (see Description; Fig. 7). The condition in PULR 09, PVL 3870, and PVL 3871 resembles that of a probable juvenile of the early sauropodomorph dinosaur *Pampadromaeus barberenai* (Müller et al., 2017), but it contrasts with the proximally flatter and more inturned femoral head of the more mature holotype specimen of this species (ULBRA-PVT016). Müller et al. (2017) interpreted this globose femoral head of the juvenile *Pam. barberenai* as a result of incomplete ossification of the proximal epiphysis, and the same could be the case if the sampled specimens of *Lago. talampayensis* (PULR 09, PVL 3870, 3871) are all juveniles. However, the absence of specimens of *Le. admixtus* or other dinosauromorphs in the Chañares Formation with an intermediate condition between a strongly convex and nearly flat proximal

Figure 7. Comparison of dinosauromorph femora from the Chañares Formation in A–D. lateral; E. posterolateral views. A. *Lagosuchus talampayensis* (PULR 09, holotype); B. *Lago. talampayensis* (PVL 3871, referred specimen, mirrored); C. *Lago. talampayensis* (PVL 3870, referred specimen); D. *Pseudolagosuchus major* (PULR 053, referred specimen, mirrored); E. *Lagerpeton chanarensis* (PVL 4619, referred specimen). A, C, E. Right femora; B, D. left femora. *Scale bars:* 5 mm.

surface of the femoral head does allow, in our opinion, interpreting the autapomorphic femoral head of *Lago. talampayensis* as ontogenetically related. Nevertheless, there are other—very likely not ontogenetically related—differences between *Lago. talampayensis* and *Le. admixtus* that still support their taxonomic distinctiveness, such as the presence in the former species of a distinctly proportionally smaller skull, coracoid foramen traversing the bone, ilium without brevis fossa, and shorter pubes (Arcucci, 1987; Sereno and Arcucci, 1994; Novas, 1996). New and more complete specimens, complemented with paleohistological analyses to assess ontogenetic stages, seem to be necessary to test the hypothesis that there is

a single species in the currently available sample of dinosauriform specimens of the Chañares Formation (Bonaparte, 1995).

We conclude that the above-discussed autapomorphies and unique combination of character states indicate that *Lago. talampayensis* is a valid species and that "*Marasuchus*" and "*M. lilloensis*" are subjective junior synonyms of *Lagosuchus* and *Lago. talampayensis*, respectively. This taxonomic scheme has been previously proposed by Bonaparte (1995).

Intraspecific Variation in *Lago. talampayensis*

A number of morphological differences between PULR 09 and specimens previously

included in the hypodigm of "*M. lilloensis*," some of them highlighted by Sereno and Arcucci (1994), deserve discussion. The base of the scapular blade of the holotype of "*M. lilloensis*" (PVL 3871) is proportionally broader anteroposteriorly than that of PULR 09, but also than in PVL 4672—a specimen referred to this species by Sereno and Arcucci (1994). The deltopectoral crest of PULR 09 extends along 31% of the length of the humerus, but along 40% in PVL 3871. The length of the radius and ulna is 65% of that of the humerus in PULR 09, whereas this ratio exceeds 72% in PVL 3871 (Sereno and Arcucci, 1994). The femoral head of PULR 09 is subtly oriented more proximomedially than in PVL 3871 and a referred specimen of "*M. lilloensis*" (PVL 3870). Metatarsal I of PULR 09 is longer than metatarsal V, but the reverse condition is present in PVL 3870. We currently ignore the ontogenetic changes that occurred during the life history of *Lago. talampayensis* because there is not a broad sample of specimens of different ages. Thus, it is possible, but it could not be tested here, that several of the differences mentioned above could be a result of the smaller size—considering size as proxy of ontogenetic age—of PULR 09 with respect to PVL 3871 (the femur of PVL 3871 is 1.4 times longer than that of PULR 09). Exceptions seem to be the width of the base of the scapular blade, orientation of the femoral head, and proportions between the lengths of metatarsals I and V. The scapular blade is proportionally broader in PVL 3871 than in the smaller PULR 09 and, also, the similar-sized PVL 4672. The difference in the proximomedial orientation of the femoral head and relative lengths of metatarsals I and V occur in rather similar-sized individuals (the femur of PVL 3870 is 1.05 times longer than that of PULR 09). As a result, we consider that these differences could be a

consequence, of nonontogenetically related intraspecific variation.

Among the probable intraspecific differences mentioned above, the difference in proportion between the anterior stylopodium and zeugopodium of PULR 09 and PVL 3871 is particularly interesting. It is striking that femoral length represents 1.5 times the length of the humerus in both PULR 09 and PVL 3871, indicating that the shorter radius and ulna of the former specimen are a result of a shortening of the zeugopodium with respect to the humerus and hindlimb. Among Triassic dinosauriforms, a similar proportional difference between the anterior stylopodium and zeugopodium has been reported as intraspecific variation in the early neotheropod *Coelophysis bauri* (radius-ulna length ratio ranges 54%–68%; Rinehart et al., 2009). In this dinosaur, there is no clear allometric tendency among all the sampled specimens, and the difference seems to be a result of both ontogeny and a dimorphism that is retained through semaphoront stages (Rinehart et al., 2009). The very scarce record of other early dinosauriform forelimbs prevents us from exploring whether the difference between the stylopodium and zeugopodium can be explained by allometric growth in *Lago. talampayensis*. Thus, again, a richer sample of specimens of *Lago. talampayensis* will seemingly be the key to improving our knowledge of these morphological variations.

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